Effects of agricultural management practices on earthworm populations and crop yield: validation and application of a mechanistic modelling approach

A.S.A. Johnston[a*], R.M. Sibly[a], M.E. Hodson[b], T. Alvarez[c], P. Thorbek[d].

[a] A.S.A. Johnston, School of Biological Sciences, University of Reading, UK, a.s.a.johnston@pgr.reading.ac.uk
[a] R.M. Sibly, School of Biological Sciences, University of Reading, UK, r.m.sibly@reading.ac.uk
[b] M.E. Hodson, Environment Department, University of York, UK, mark.hodson@york.ac.uk
[c] T. Alvarez, EcoRisk Solutions Ltd., Norwich, UK, tania.alvarez@ecorisksolutions.co.uk
[d] P. Thorbek, Environmental Safety, Syngenta Ltd., Bracknell, UK, pernille.thorbek@syngenta.com

* Corresponding Author:
a.s.a.johnston@pgr.reading.ac.uk
School of Biological Sciences,
University of Reading,
Reading, RG6 6AS
Tel +44 (0)7592600201

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Summary

1. There is little consensus on how agriculture will meet future food demands sustainably. Soils and their biota play a crucial role by mediating ecosystem services that support agricultural productivity. However, a multitude of site-specific environmental factors and management practices interact to affect the ability of soil biota to perform vital functions, confounding the interpretation of results from experimental approaches. Insights can be gained through models which integrate the physiological, biological and ecological mechanisms underpinning soil functions.
2. We present a powerful modelling approach for predicting how agricultural management practices (pesticide applications and tillage practices) affect soil functioning through earthworm populations. By combining energy budgets and individual-based simulation models, and integrating key behavioural and ecological drivers, we accurately predict population responses to pesticide applications in different climatic conditions.
3. We use the model to analyse the ecological consequences of different weed management practices. Our results demonstrate that an important link between agricultural management (herbicide applications and zero, reduced and conventional tillage) and earthworms is the maintenance of soil organic matter (SOM).
4. We show how zero and reduced tillage practices can increase crop yields while preserving natural ecosystem functions. This demonstrates how management practices which aim to sustain agricultural productivity should account for their effects on earthworm populations, as their proliferation stimulates agricultural productivity.
5. ***Synthesis and Applications.*** Our results indicate that weed management that relies on tillage has longer term effects on soil biota than pesticide control, if the herbicides have short dissipation times. If pesticides known to be toxic to earthworms are

applied, the risk of exposure will be reduced if irrigation is stopped around application time or if application is carried out during dry periods. Similarly, if the organic content of the soil is increased the recovery rate of earthworm populations can be increased. However, effects are not necessarily additive and the impact of different growing practices on earthworms will depend on their timing and the environmental conditions. Our model can be used to estimate the overall impact of different combinations of crop management activities in different regions to explore how earthworm populations respond. If our models are linked to crop yield models the costs and benefits of different crop solutions for both yields and biota could be estimated and aid optimisation of the trade-off between different ecosystem services.

Keywords: agriculture; earthworm; ecosystem services; energy budget; pesticides; population modelling; tillage; weed management.

Introduction

Fertile soils are a crucial element of food security, providing the basic foundation of agroecosystems. However, soil erosion exceeds soil formation in many arable systems (Amundson *et al.* 2015). Indeed, declining crop yields indicate diminishing returns from fertiliser applications (Tilman *et al*. 2002), whilst current mechanical practices (e.g. tillage) continue to accelerate soil erosion (Montgomery 2007). At the same time, the provision of essential ecosystem services from soils (e.g. soil formation, nutrient cycling and food production; MEA 2005) depends on the regulatory functions of soil biota (Dominati *et al.* 2010; Amundson *et al.* 2015).). Accordingly it has been argued that sustainable agricultural intensification could be achieved through management practices (e.g. reduced tillage and pesticide applications) which preserve the essential functions of keystone soil species (Badgley *et al.* 2007).

Keystone species in soils include earthworms, which act as ecosystem engineers both directly through digestion and burrowing activities and indirectly by encouraging other beneficial soil organisms (Blouin *et al.* 2013; Jones *et al.* 1994; Darwin 1881). They often constitute the most abundant animal biomass in terrestrial ecosystems (Lavelle & Spain 2001) and are important indicators of soil quality (Doran & Zeiss 2000). Management practices which optimise soil environmental conditions (e.g. soil organic carbon (SOM) and soil moisture) also stimulate earthworm biomass production (Lavelle *et al.* 2006). In turn the effects of earthworm activity on soil aggregate stability, nutrient cycling and soil carbon dynamics improve crop yields (Brown *et al.* 1999; Scheu 2003).

Although changes in agricultural management may increase the soil biota biomass, sustainable yield increases are unlikely to be achieved long-term in the absence of external inputs. For example, weed control is necessary to decrease competition with crop plants. In addition, different agricultural systems affect the soil biota in diverse ways, which depend on specific combinations of farm management practices and environmental factors. This makes the results of experimental field studies hard to extrapolate for different environmental conditions. Thus, tools are needed to better predict how land management practices affect the provision of ecosystem services through their effects on important soil biota.

Population models have been used to predict how populations will respond to anthropogenic environmental change, but most ignore the underlying mechanisms. Many focus only on the level of populations or individuals, rather than representing the processes which link both levels of biological organisation (Forbes *et al.* 2008). Whereas statistical models or models

that merely project current situations (e.g. matrix models) are little suited for extrapolating outside the range they have been parameterised for, mechanistic models that capture key biological, physiological and ecological mechanisms underpinning system functioning have much better predictive power (Grimm & Railsback 2012). Such models could offer greater insights into how management practices alter ecosystem functioning through effects on individual organisms (e.g. Railsback & Johnson 2014).

The combination of energy budget and individual-based population models has shown promise for explaining population dynamics from individual physiological mechanisms in aquatic systems (Martin *et al.* 2013). In terrestrial systems spatio-temporal dynamics of both individuals and their environment must be modelled since they crucially affect population dynamics (Harrison 1993). Here, we present a novel mechanistic model for predicting effects of agricultural management on earthworm populations that in turn allows us to predict crop yields using a crop yield–earthworm biomass relationship derived using literature data. We use the model to investigate agricultural weed management practises.

To incorporate the multiple factors (e.g. climate, soil type, intensity, timing and type of management practices) needed to better understand the relationship between management practices and earthworm populations in spatially explicit soil profiles we developed a novel individual-based energy budget model (Johnston *et al.* 2014a, 2014b). Here, we validate the published model presented in Johnston *et al.* (2014b) by comparing model outputs with independent field data and explore the effects of different weed management scenarios, including pesticide application and tillage practices, with the aim of linking ecosystem-level functions to dynamic populations.

Methods

The Model

We apply a previously published model of earthworm distribution and abundance in soil profiles to simulate population dynamics in different agricultural management scenarios. We model *Aporrectodea caliginosa*, the dominant earthworm species in conventionally managed arable agroecosystems. The model combines an energy budget model and an individual-based simulation model. For full details of the energy budget model for the earthworm *Eisenia fetida* see Johnston *et al.* (2014a) and development of the model for field populations of *A. caliginosa* see Johnston *et al.* (2014b). The Netlogo programme code is provided in Appendix S1 of the Supporting Information. The implementation of the model is copyrighted to Alice Johnston and licensed under the GNU General Public Licence.

The energy budget model describes how individuals ingest food from their environment and allocate available energy to life cycle processes (maintenance, reproduction, growth and energy storage) (Fig. 1).

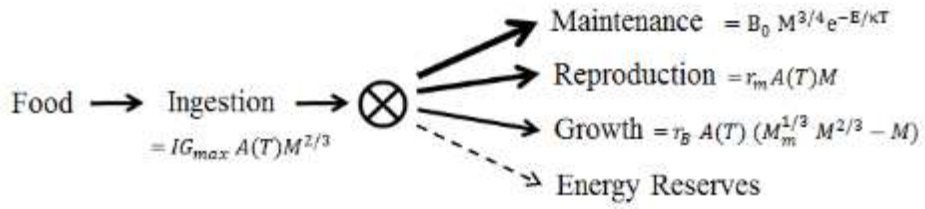

Fig. 1. Structure of the energy budget model. The thickness of solid arrows indicates priorities for allocation of energy obtained from food. Equations show maximum daily allocation rates which depend on individual

bodymass, *M*, temperature, *T*, and parameters as defined in Table 1 in Appendix S2. *A*(*T*) is the Arrhenius function of temperature (Johnston et al., 2014b).

Energy budget parameters were calculated from laboratory data relating *A. caliginosa* growth and reproduction rates under optimal environmental conditions (Table 1 in Appendix S2). When individuals experience sub-optimal conditions (e.g. low temperature or food availability) metabolic rates are reduced (Johnston *et al.* 2014b).

Model soil profiles spanned 2 m (horizontal) × 0.5 m (vertical), comprising 5 × 5 cm soil patches characterised by temperature, water content, texture, bulk density and soil organic matter (SOM; where SOM = soil organic carbon (SOC) × 1.42 after Guo & Giffard 2002) content. Daily fluctuations in soil conditions were modelled according to observed seasonal and vertical patterns (Fig. 2; for full details see Johnston *et al.* 2014b).

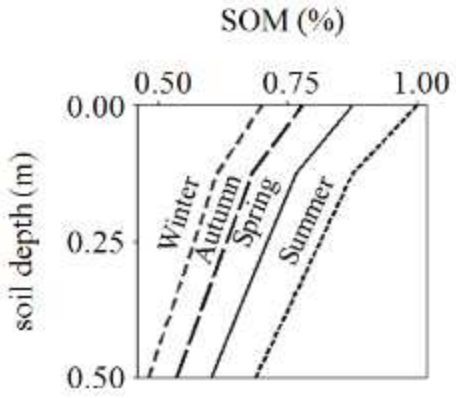

Fig. 2. Modelled soil organic matter (SOM) dynamics with soil depth, presented as mean proportions of the maximum measured value.

Individuals move through the soil profile in response to food quality and soil water content in neighbouring soil patches. In general, soil water increases and food quality (SOM) decreases with depth, causing the vertical distribution of the population to change in response to daily environmental fluctuations. Aestivation (a period of inactivity) is triggered when soil conditions become too dry: individuals then use their energy reserves to pay the energetic costs of maintenance (Johnston *et al.* 2014b).

Pesticide Effects

Pesticides were applied to soil patches and effects on individuals were modelled according to dose-response curves which specify relationships between pesticide concentration and metabolic parameters (growth constant (r_B), maximum rate of energy allocation to reproduction (r_m) and survival). Full details of the dose-response curve methods are presented in Johnston *et al.* (2014a). Here, the dose-response curves were parameterised for effects of the fungicide carbendazim and a hypothetical herbicide on *A. caliginosa*. Carbendazim is used as a toxic standard in risk assessment field trials due to its acute effects on earthworm populations, and so provides a useful pesticide application scenario to validate our model. We use a hypothetical herbicide to model herbicide applications realistic of general agricultural practice. The curves are of the form:

$$R(C) = e^{kC} \qquad \text{Eq. 1}$$

where *R(C)* is the response at concentration *C* (mg/kg) and *k* is the toxicity coefficient. *k* was estimated for carbendazim by a least sum of squares fit to the data of Lofs-Holmin (1982), recorded as a proportion of the control (Fig. 3a). Although the data of Lofs-Holmin (1982) are for benomyl, carbendazim is its principle metabolite and the two are used interchangeably in regulatory studies as toxic standards. Moreover, whilst alternative methods such as the Hills equation (Hill, 1910) provide a slightly better fit to the data, these introduce additional parameters and our aim here is to provide a simple model of pesticide effects. Full details and justifications are provided in Appendix S3. We also modelled effects of a hypothetical herbicide using fictitious data (Fig. 3b). The response curves specify how r_B and r_m are affected by the pesticide relative to values in control conditions given in Table 1 in Appendix S2. Estimated values of the toxicity coefficient (*k*) for growth, reproduction and survival are -2.66,-1.28 and -1.05 for carbendazim (Fig. 3a and Appendix S3) and -0.06,-0.04 and -0.006 for the hypothetical herbicide (Fig. 3b), respectively. We also assumed that carbendazim leads to an increase in maintenance costs, either to eliminate the toxin or repair toxic damage (e.g. Givaudan *et al.* 2014), assuming a linear relationship between the maintenance parameter B_0 and *C* following: $B_0(C) = B_0(4.5 \times C)$.

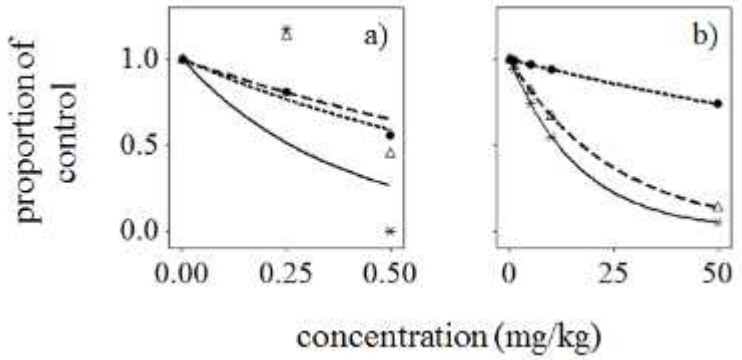

Fig. 3. Modelled dose-response relationships specifying the effects of pesticide concentrations on life cycle traits for: a) carbendazim derived from the laboratory data of Lofs-Holmin (1982) and b) a hypothetical herbicide on growth (asterisks, solid line), reproduction (triangles, dashed line) and survival (circles, dotted line) represented as a proportion of the life cycle trait in control conditions.

Tillage Effects

Effects of zero (our control treatment), reduced and conventional tillage to a soil depth of 0, 10 and 20 cm respectively (Kassam et al., 2009) were simulated on both earthworm mortality and soil physical conditions (soil water content, SOM and bulk density). SOC is 0.7 – 1.8 kg C/m^2 less in the top 15 cm of soils under conventional tillage than in zero tillage systems (Kern & Johnson 1993). Soil bulk density follows a similar pattern, declining by around 0.13 g/cm^3 in the top 30 cm of soils under conventional tillage compared to zero tillage (Balesdent, Mariotti & Boisgontier 1990). These declines in soil properties under tillage are represented as a proportion under zero tillage control conditions in Figure 4. To model these effects we assume that SOM and bulk density are altered to soil depths of 10 cm for reduced and 20 cm for conventional tillage practices. Moreover, soil properties decline or increase exponentially with time during the use of tillage practices and after the cessation of tillage, respectively (Francis & Knight 1993). Based on these studies, SOM and bulk density, which in the model together represent food availability and quality, decrease with time under consecutive tillage years and increase after cessation of tillage practices as outlined in Fig. 4. We also assumed a soil temperature increase of 0.70 ºC and soil water content decrease of 0.04 cm/cm^3 following tillage (Pelosi *et al.* 2008). Direct earthworm mortality during tillage is assumed to be 50 % in the tilled soil layer for adults and juveniles (Marinissen 1992).

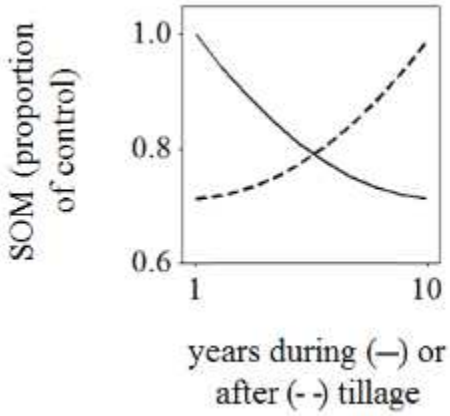

Fig. 4. Modelled effects of tillage on SOM and bulk density over time, represented as a proportion of the soil property under zero tillage control conditions.

Simulation Experiments

The model was set up to simulate experiments to validate the model or to explore effects of different agricultural management approaches on ecosystem services. In each experiment model populations were stabilised for 50 years with the relevant environmental measurements before results were recorded as the mean of four model replicates for each time point.

Model Validation

The model was set up to mimic the conditions of independent field trials used to validate the model. In the field trials earthworm populations were monitored in control conditions and in response to toxic-standard (carbendazim) applications.

Control Conditions

Field trials were conducted in Germany (G1, G2, G3) (Klein 2010a, b & c) and Spain (S1, S2) (Klein 2013a & b), under varied soil and climatic conditions (Table 1 and see Appendix S4 for full details of the environmental and management conditions for each field study). Soil temperature and water content measurements were taken directly from the study reports (see Fig. 1 in Appendix S4); SOM measurements (used to calculate food energy content, E_x) were used to model seasonal and vertical fluctuations in food quality (Fig. 2). Soil water content and texture were both used to calculate the soil water potential of model patches, which together with SOM drives movement of individuals through the soil profile (details given in Johnston *et al.* 2014b).

Table 1. Variations in mean annual soil conditions between the five independent field trials conducted in Germany (G1, G2, G3) or Spain (S1, S2). Soil measurements present the annual mean and standard deviation for the top 5 cm of the soil profile (N = 365).

	G1	G2	G3	S1	S2
Soil texture	Poor clay silt	Loamy Silt	Loamy Silt	Sandy loam	Sandy loam
SOM (%)	2.04 ±0.31	2.31 ±0.36	2.58 ±0.40	6.04 ±0.93	3.35 ±0.52
Soil temperature (°C)	9.81 ±7.18	10.38 ±6.94	8.88 ±7.26	13.18 ±4.61	12.72 ±4.72
Soil water potential (-kPa)	18.21 ±9.44	9.83 ±3.20	6.69 ±1.33	14.60 ±4.14	16.63 ±10.44

Carbendazim Applications

Toxic-standard simulations followed control conditions as outlined above. Carbendazim application was in April or May in the German field trials and June in the Spanish field trials. Carbendazim was applied at a rate of 10, 000 g a.i./ha to the top 5 cm of the model soil profile on the specified dates. Post-application concentrations were modelled using simple first-order exponential degradation. The time taken for the pesticide to degrade to 50 % of the application rate (DT_{50}) was taken as 20 days (Jones *et al.* 2004; Li & Nelson 1985).

Goodness of Fit

The goodness of fit of the model outputs to independent data is measured using the coefficient of determination (R^2). R^2 values were calculated as: 1 – (residual sum of squares)/(total sum of squares)), with values closer to 1 representing better agreement between observed and predicted values. As our model parameter values are not estimated from the data conventional statistical methods of assessing R^2 values are not applicable here. We suggest that values of $R^2 > 0.5$ indicate a good fit (Johnston et al., 2014b).

Model Application: Weed Management Scenarios

Weed management scenarios were investigated by simulating hypothetical herbicide applications accompanied by zero, reduced or conventional tillage. The environmental conditions (soil temperature, water content and SOM dynamics) used for these simulations were those of German field trial G1, (see Table 1 and Appendix S4).

Herbicides

Hypothetical herbicide applications were simulated at concentrations producing 10 and 20 % effects on individual life cycle processes (growth, reproduction and mortality as in Fig. 3b). These magnitudes of effect are realistic for general agricultural practice as higher effects would likely fail the initial tiers of ecological risk assessment. The herbicide was applied to the top 5 cm of the model soil profile in May, with a DT_{50} value of 100 days.

Tillage

Zero, reduced and conventional tillage was simulated to a soil depth of 0, 10 and 20 cm respectively, with direct effects on earthworm mortality (50 %) and indirect effects on soil conditions (SOM, bulk density, soil water content and temperature) in the tilled layers.

Model Prediction of Crop Yield

We modelled how the different weed management scenarios described in the previous section affected earthworm populations and crop yield. The modelled regression fit to published data (selected from the literature irrespective of tillage practices and herbicide applications) on the relationship between earthworm population biomass and crop yield is presented in Fig. 5. Studies included in the regression analysis were limited by the available data on earthworm biomass and crop yields measured under the same conditions. Full details of the database are presented in Table 1 of Appendix S5. From these relationships we estimated the potential of different tillage and herbicide practices to influence agricultural productivity (crop yields) via modelled earthworm biomass under the different weed management scenarios modelled here and the regression relationship shown in Fig. 5.

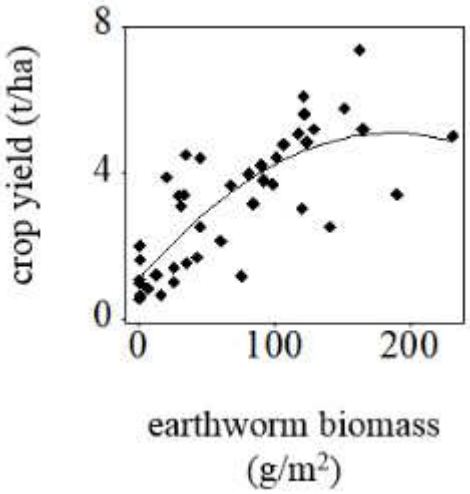

Fig. 5. Modelled relationship between crop yield and earthworm biomass (R^2=0.63, $p < 0.001$). See Table 1 in Appendix S5 for full study details.

Results

Model Validation

We validated our model by comparing its outputs with records of earthworm population biomass in five independent field trials, in each of which a toxic-standard pesticide application using carbendazim was paired with a control (Fig. 6). The earthworm population biomass model outputs are available in the University of Reading repository CentAUR (http://centaur.reading.ac.uk/). The model provides excellent agreement with the field data in all control populations and in four out of five toxic-standard populations. The field trials differed in their environmental conditions; three were conducted in Germany (Figs 6a – f) and two in Spain (Figs 6g – j) (Table 1).

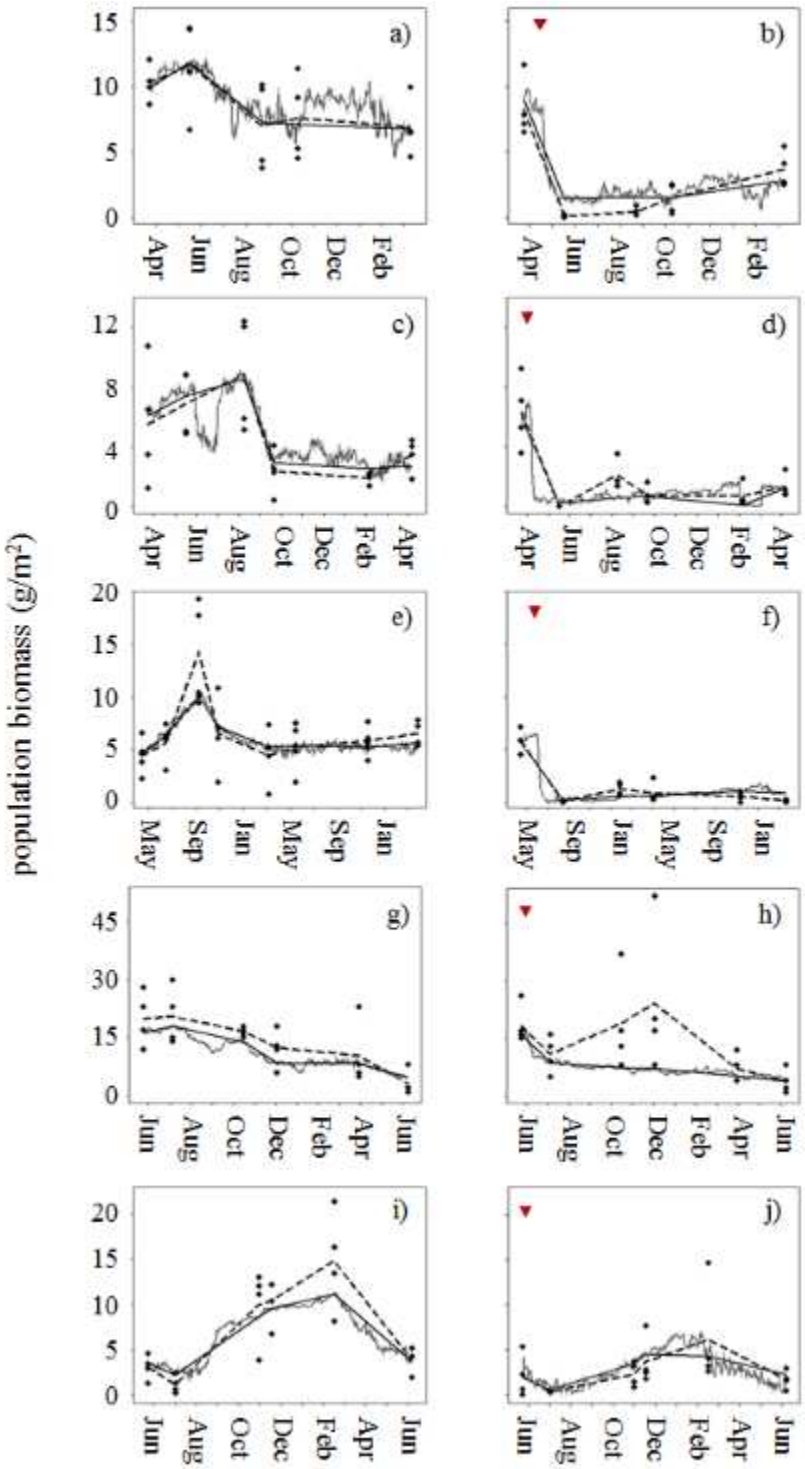

Fig. 6. Model validation against independent field data, presenting comparisons of model outputs (grey lines represent the continuous model output and the solid black line is the mean for the sample dates) and independent field data (symbols represent replicates and the dashed line is the mean) of earthworm population biomass in control conditions (left-hand panels) and in response to carbendazim (10,000 g/ha) (date of application represented by the triangle;(right-hand panels). Data and model simulations are of three German: G1 (a, b), G2 (c, d), G3 (e, f), and two Spanish: S1 (g, h) and S2 (i, j) field trials.

Model results can be explained in terms of the way individuals move; the spatial choice of modelled individuals is a trade-off between favourable soil water and food quality conditions. When soil is sufficiently moist, individuals move to more energy rich soil towards the surface (Johnston *et al.* 2014b). The vertical distribution of individuals in the soil profile then determines how exposed the population becomes to management practices. Thus, the toxic effects of pesticide applications in the top 5 cm of the soil profile occur when environmental conditions are sufficiently favourable (wet) for earthworm movement to and within surface layers. Accordingly, the variation in population-level effects in Fig. 6 was a consequence of different soil water conditions during pesticide application. For instance, favourable soil water conditions during pesticide applications in Germany increased population exposure to pesticide applications at the soil surface in April or May (Figs 6b, d and f). In contrast, dry soil conditions during pesticide applications in Spain (Fig. 6j) reduced population exposure, and our model captures the following recovery in population biomass.

As our model assumes that conditions in the toxic-standard treatment and control were the same – except for application of carbendazim – the model was not able to replicate the population increase observed in the toxic standard of field trial S1 in October and December (Fig. 6h). Due to the unusual observation of increased population biomass following application of a very toxic pesticide the results of field trial S1 are omitted from the overview of the model's fit to the data presented in Fig. 7a ($R^2 = 0.92$).

We tested the sensitivity of model outputs to the removal of model components by simulating the four field trials without pesticide effects on mortality (Fig. 7b) or by excluding aestivation (Fig. 7c) and directional movement (Fig. 7d) and found that all model components were necessary to achieve good model agreement with the independent data.

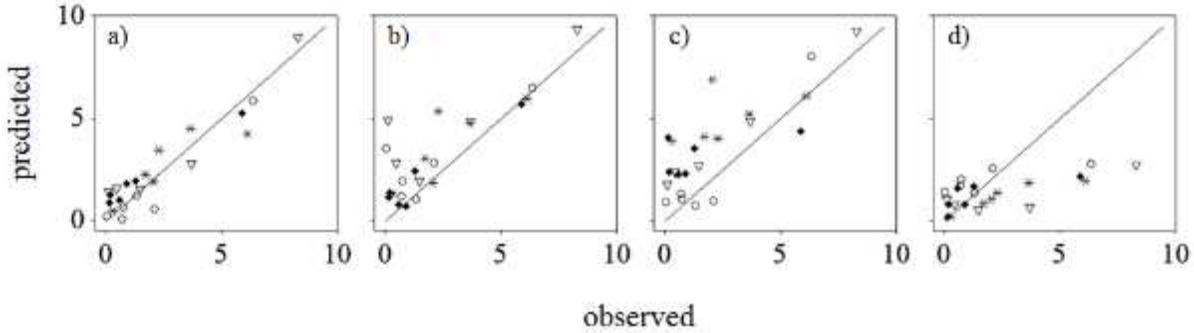

Fig. 7. Predicted versus observed values for mean earthworm population biomass (g/m^2) responses to carbendazim in the three German (G1:▽, G2:◆, G3:○) and one Spanish (S2:✳) field trial/s for a) the presented model ($R^2 = 0.92$), b) for when pesticide effects on mortality are removed ($R^2 = 0.68$), c) when aestivation due to dry soil conditions is excluded ($R^2 = 0.51$), and d) when movement is assumed to be random ($R^2 = 0.50$).

This extensive validation showed the model accurately predicts earthworm population responses to pesticide applications under field conditions.

Model Application: Weed Management Scenarios

Here, we present model simulation results for seven different weed management scenarios: zero, reduced and conventional tillage practices, each with or without applications of a hypothetical herbicide at 10 or 20 % effect (on growth, reproduction and survival) concentrations (Fig. 8).

All of the simulated weed management systems resulted in initial declines in earthworm biomass, but populations stopped falling by the end of the 10 year application period (Fig. 8). Ten years after cessation of the treatments, earthworm populations that had experienced zero tillage and herbicides had fully recovered (green and blue lines), those experiencing reduced and conventional tillage had not (orange and red lines).

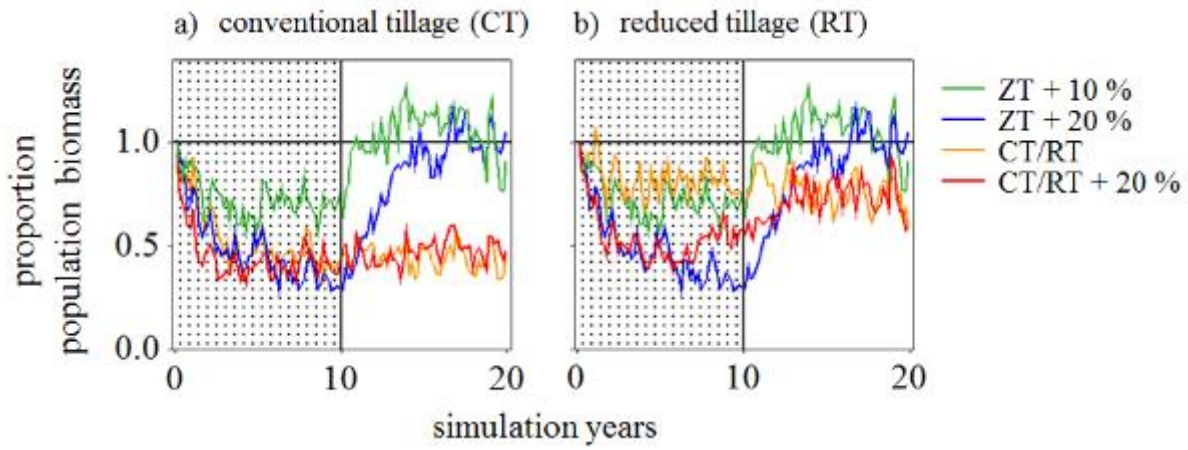

Fig. 8. Effects of weed management practices on earthworm population biomass, presented as a proportion of the population under zero tillage conditions without herbicide applications (black horizontal line). There were two tillage treatments: a) conventional (CT) and b) reduced (RT) tillage. Each was applied either without herbicide (orange lines) or with herbicide applications at 20 % effect concentrations (red lines), and compared to the effects of zero tillage (ZT) combined with herbicide applications at 10% (green line) or 20 % (blue line) effect concentrations. Tillage and/or herbicides were applied annually for 10 years (shaded area), after which the treatments were stopped and populations observed for a further 10 years.

Earthworm populations took longer to recover after the ten year application period in the conventional tillage scenarios than the other weed management scenarios because conventional tillage has negative effects on soil physical conditions. A reduction in the SOM and soil water content of tilled soils makes the environment less favourable for earthworm activity, and these conditions become increasingly adverse with tillage depth. In contrast, herbicide applications have direct effects on earthworm life cycle processes (survival, growth and reproduction) and these effects depend on individuals becoming exposed in the surface layers of soil. Hence, as in the model validation results in Fig. 6, herbicide effects are subject to the relationship between environmental conditions (e.g. SOM and soil water conditions) and individual behaviour (e.g. movement and aestivation), together with herbicide toxicity.

When herbicides are applied alongside conventional tillage (Fig. 8a), the population's exposure to pesticides was altered by the effect of tillage practices on soil conditions. Less favourable conditions in the top 20 cm of the soil profile reduced population exposure to herbicide applications in the top 5 cm, which then had no additional effects, compared to tillage alone. In contrast, at reduced tillage to a depth of 10 cm, the effects of herbicides together with tillage were smaller than herbicide applications with zero tillage after 10 years of treatment (red vs blue lines in Fig. 8b). Here, mechanical disturbance reduced the population-level effects of herbicide applications by making the surface soil layers less favourable and direct earthworm mortality, thus reducing herbicide exposure. Nevertheless,

population recovery was slower after tillage ceased due to the long-term effects of mechanical disturbance on soil organic matter (Figure 4). Thus, management intensity drove the overall population-level effect, with population recovery declining as depth of tillage and level of herbicide application increased (Figs 8 and 9).

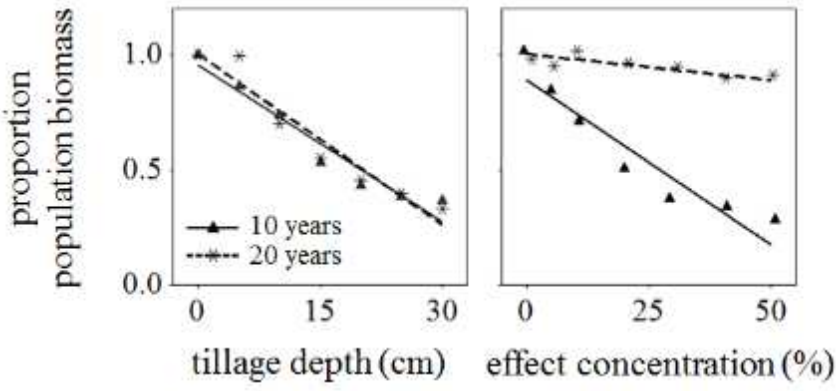

Fig. 9. Effects of increasing tillage depths (left) and herbicide effect concentrations under zero tillage (right) on modelled earthworm population biomass relative to control after 10 years of annual applications (triangle symbols and solid line) and 10 years after the cessation of management practices (20 years, asterisk symbols and broken line).

Model Prediction of Crop Yield

The beneficial effects of larger earthworm populations on crop yields under conservation (reduced and zero) tillage practices with hypothetical herbicide applications causing 20 % effects were modelled using the relationships outlined in Fig. 5. Here, we make the assumption that the relationship between earthworm biomass and crop yield is causative. However, these mechanisms are not yet fully understood and other potential relationships are mentioned in the Discussion. Earthworm biomass increases of 48 % and 83 % led to crop yield improvements of 21 % and 35 % under reduced and zero tillage practices, compared to conventional tillage systems, respectively (Table 2). These values were hard to validate because of inconsistencies in reported changes in soil conditions and crop yields with tillage practices because of unknown effects of climate, soil type and other management practices.

Table 2. Estimated effects of various tillage practices with 20% effect concentration herbicide applications on earthworm biomass as modelled here and crop yields. Relative input costs and carbon emissions for the different management scenarios are taken directly from Harper (1996) and Kern & Johnson (1995).

Tillage practice	Earthworm biomass (g/m^2)	Crop yield (tonnes/ha)	Input Cost (US$/ha/year)	Carbon emissions (kg C/ha/year)
Conventional	27.1	2.18	16.05	53
Reduced	40.0	2.63	16.47	45
Zero	49.7	2.95	14.76	29
Reference	Our model	Fig. 5	Harper (1996)	Kern & Johnson (1995)

Discussion

Validation of our model showed excellent model fits to earthworm population dynamics from independent field trial data for both toxic-standard and control scenarios under different climatic conditions. We argue that the model predicted population dynamics accurately under diverse field conditions because it captured the key mechanisms driving the physiological and behavioural ecology of earthworms. Parameter values for individuals were derived from standardised laboratory conditions, and so good model agreement with independent field studies under different environmental conditions demonstrates the model's ability to extrapolate beyond its parameterisation range (Fig. 6). Although our approach was complex in comparison to more classical models, our fits to independent data were excellent (R^2 = 0.92). Reduced agreement between the model and data when key processes were omitted emphasise the importance of including the mechanisms underpinning biological complexity (Fig. 7).

Simulation models are needed to deliver useful predictions about systems under novel conditions (Grimm & Railsback 2012). However, a common perception is that increasingly realistic (and therefore complex) models become tied to specific scenarios, whilst simpler models provide more generic insights (Evans *et al.* 2013). This view ignores the fact that when the interactions between ecological drivers and individual physiology are represented, numerous extrapolations between environmental conditions are possible. Mechanistic models like the one presented here are thus both realistic and generic. Similar realism and generality have been achieved by Martin *et al.* (2013) but in simpler environments lacking spatial heterogeneity, which here affects population exposure through individual behavioural decisions.

Weed management and soil fertility are at the heart of successful farming (Lewis *et al.* 1997). Yet there is often a trade-off between them because traditional weed management through frequent tillage diminishes soil biota and soil fertility. Alternatively under conservation agriculture the use of selective herbicides is necessary, but these also have the potential to affect soil biota. Our simulations of different weed management scenarios show that in contrast to herbicides, effects of different tillage practices on earthworms are driven by SOM losses at different soil depths, alongside direct mortality, which is more long lasting and detrimental to soil biota (Fig. 8). These results demonstrate how the spatio-temporal extent of management induced soil changes drives soil biota population level responses (Fig. 9). Moreover, a lack of additive effects when herbicides are applied alongside tillage, compared to tillage practices alone, indicate how the effects of single management practices on the biota can outweigh those of others. Hence, it is important to assess different management practices together to understand the impact of agricultural systems on soil functioning. These results depend on the environmental fate of the pesticide (which controls the vertical and temporal exposure profile) as well as the toxicity of applied pesticides in specific

environmental situations. Thus, simulations for particular earthworm communities, pesticides, soil types and climate properties may be needed. Nevertheless, these results do suggest that the preservation of SOM should be brought to the forefront of sustainable production systems. Although this is not a new discovery (Kassam *et al.* 2009), our model provides the means for optimising farm management solutions for different regions, crops and growing systems.

Ecosystem services are a key concept in agroecosystem management (e.g. EFSA 2010; Galic *et al.* 2012). Still, current risk assessments of management systems often only consider one factor at a time, whilst farming faces a multitude of ongoing difficulties with pest, pathogen and weed control as well as herbicide resistance in zero tillage systems (Owen & Zelaya 2005). Our results highlight that investigation of single factors (e.g. herbicides) can lead to practices that cause greater risks (e.g. tillage) being overlooked. To further illustrate the utility of the model for agricultural managers, we predict how the multiple effects of different weed management practices on soil functioning alter the delivery of a specific provisioning ecosystem service (crop yields) (Table 2). Using a relationship derived from literature data on earthworm populations and crop yields (Fig 5 and Table 1 in Appendix S5), our model predicts that crop yields could increase by an average 28 % using zero or reduced tillage together with herbicides. This agrees well with observations that earthworm presence in agroecosystems lead to an average 25 % increase in crop yield (van Groenigen *et al.* 2014). However, these calculations are somewhat crude, ignoring the multiple feedbacks between biological populations and the physical environment.

Although positive relationships have been observed between earthworm population abundance and SOC stocks, water regulation and nutrient mineralization, the specific mechanisms underlying relationships between earthworms and plant production are not fully understood (van Capelle, Schrader & Brunotte 2012). The recent meta-analysis by van Groenigen *et al* (2014) suggested that earthworms stimulate plant production through the release of nitrogen from crop residues and SOM, whilst Spurgeon *et al* (2013) found that the proliferation of earthworm communities under reduced tillage, compared to conventional systems, increased the provision of soil structure and hydrology-related ecosystem services. However, observations on the effect of zero and reduced tillage on crop yields are highly variable globally (Pittelkow *et al.* 2015). Integration of the feedbacks between management practices, soil properties and crops in modelling approaches like the one presented here could elucidate the underlying mechanisms. Although we do not integrate these feedbacks here our estimates of earthworm effects on crop yield serve to illustrate how better soil management (e.g. reduced tillage and herbicide applications) could increase crop yields whilst preserving natural ecosystem functions and reducing fuel and herbicide costs (Table 2).

Soil erosion in agricultural systems is a major threat to food security (Amundson *et al.* 2015) and earthworms are key ecosystem engineers providing important benefits to soil health (Blouin *et al*. 2013). Our results indicate that tillage has long term effects on soil biota via direct mortality and structural changes to the soil. In contrast, weed management by herbicides may have toxic effects but these are, at least under some circumstances, of a shorter duration. If pesticides known to be toxic to earthworms are applied, the risk of exposure will be reduced if irrigation is stopped around application time or if application is carried out during dry periods. Similarly, if the organic content of the soil is increased the recovery rate of earthworm populations can be increased. However, effects are not always additive and the impact of different crop management practices on earthworms will depend

on both timing and environmental conditions. Our model can be used to estimate the overall impact of different crop solutions in different regions to see which ones pose the least overall risk to earthworm populations. Linking of our model to crop yield models would support estimates of the costs and benefits of different crop solutions and help optimise the trade-off between different ecosystem services.

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References

Amundson, R., Berhe, A.A., Hopmans, J.W., Olson, C. Sztein, A.E. & Sparks, D.L. (2015) Soil and human security in the 21st century. *Science*, **348** (6235): DOI: 10.1126/science.1261071.

Badgley, C., Moghtader, J., Quintero, E., Zakem, E., Chappell, M. J., Aviles-Vazquez, K., Samulon, A. & Perfecto, I. (2007) Organic agriculture and the global food supply. *Renewable Agriculture and Food Systems*, **22**, 86-108.

Balesdent, J., Mariotti, A. & Boisgontier, D. (1990) Effect of tillage on soil organic carbon mineralization estimated from ^{13}C abundance in maize fields. *Journal of Soil Science*, **41**, 587-596.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D. & Brun, J.-J. (2013) A review of earthworm impacts on soil function and ecosystem services. *European Journal of Soil Science*, **64**, 161-182.

Brown, G.G., Pashanasi, B., Villenave, C., Patron, J.C., Senapati, B.K., Giri, S., Barois, I., Lavelle, P., Blanchart, E., Blakemore, R.J., Spain, A.V. & Boyer, J. (1999) Effects of earthworms on plant production in the tropics. *Earthworm Management in Tropical Agroecosystems* (eds P. Lavelle, L. Brussaard & P. Hendrix), pp. 87-148. CAB International, Wallingford.

Darwin, C. (1881) *The formation of vegetable mould through the action of worms with observation on their habits*. London, Murray.

Dominati, E., Patterson, M. & Mackay, A. (2010) A framework for classifying and quantifying the natural capital and ecosystem services of soils. *Ecological Economics*, **6**, 1858-1868.

Doran, J.W. & Zeiss, M.R. (2000) Soil health and sustainability: managing the biotic component of soil quality. *Applied Soil Ecology*, **15**, 3-11.

EFSA (European Food Safety Authority) Panel on Plant Protection Products and their Residues (PPR) (2010) Scientific opinion on the development of specific protection goal options for environmental risk assessment of pesticides, in particular in relation to the revision of the Guidance Documents on Aquatic and Terrestrial Ecotoxicology (SANCO/3268/2001 and SANCO/10329/2002). *EFSA Journal 2010*, **8**, 1821-1875.

Evans, M.R., Grimm, V., Johst, K., Knuuttila., T., de Langhe., R., Lessells, C.M., Merz., M., O'Malley, M.A., Orzack., S.H., Weisberg., M., Wilkinson., D.J., Wolkenhauer., O. & Benton., T.G. (2013) Do simple models lead to generality in ecology? *Trends in Ecology & Evolution*, **28**, 578-583.

Forbes, V.E., Calow, P. & Sibly, R.M. (2008) The extrapolation problem and how population modeling can help. *Environmental Toxicology and Chemistry*, **10**, 1987-1994.

Francis, G.S. & Knight, T.L. (1993) Long-term effects of conventional and no-tillage on selected soil properties and crop yields in Canterbury, New Zealand. *Soil & Tillage Research*, **26**, 193-210.

Galic, N., Schmolke, A., Forbes, V., Baveco, H. & van den Brink, P.J. (2012) The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems. *Science of the Total Environment*, **415**, 93-100.

Givaudan, N., Wiegand, C., Le Bot, B., Renault, D., Pallois, F., Llopis, S. & Binet, F. (2014) Acclimation of earthworms to chemicals in anthropogenic landscapes, physiological mechanisms and soil ecological implications, *Soil Biology and Biochemistry*, **73**, 49-58.

Grimm, V. & Railsback, S.F. (2012) Pattern-oriented modelling: a "multiscope" for predictive systems ecology. *Philosophical Transactions Royal Society London B*, **367**, 298-310.

Guo, L.B. & Gifford, R.M. (2002) Soil carbon stocks and land use change: a meta analysis. *Global Change Biology*, **8**, 345-360.
Harper, J.K. (1996) *Economics of Conservation Tillage*. Conservation Tillage Series Number Six. College of Agricultural Sciences. PennState. Available at: http://pubs.cas.psu.edu/FreePubs/pdfs/uc130.pdf. Accessed 19.06.14.
Harrison, S. (1993) Species diversity, spatial scale, and global change. *Biotic Interactions and Global Change* (eds P.M. Kareiva, J.G. Kingsolver & R.H. Huey), pp. 388-401. Sinauer, Sunderland, MA.
Johnston, A.S.A., Hodson, M.E., Thorbek, P., Alvarez, T., Sibly, R.M. (2014a) An energy budget agent-based model of earthworm populations and its application to study the effects of pesticides. *Ecological Modelling*, **280**, 5-17.
Johnston, A.S.A., Holmstrup, M., Hodson, M.E., Thorbek, P., Alvarez, T. & Sibly, R.M., (2014b) Earthworm distribution and abundance predicted by a process-based model. *Applied Soil Ecology*, **84**, 112-123.
Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373-386.
Jones, S.E., Williams, D.J., Holliman, P.J., Taylor, N., Baumann, J., Förster, B., van Gestel, C.A.M. & Rodrigues, J.M.L. (2004) Ring-testing and field-validation of a terrestrial model ecosystem (TEM) – An instrument for testing potentially harmful substances: fate of the model chemical carbendazim. *Ecotoxicology*, **13**, 29-42.
Kassam, A., Friedrich, T., Shaxson, F. & Pretty, J. (2009) The spread of conservation agriculture: justification, sustainability and uptake. *International Journal of Agricultural Sustainability*, **7**, 292-320.
Kern, J.S. & Johnson, M.G. (1993) Conservation tillage impacts on national soil and atmospheric carbon levels. *Soil Science Society of America Journal*, **57**, 200-210.
Klein, O. (2010a) *Mesotrione/S-Metolachlor/Glyphosate CS (A15189G) - a field study to investigate effects on the earthworm fauna on bare earth in southern Germany.* Eurofins Report Number S09-00999.
Klein, O. (2010b) *Tefluthrin GR (A13226J) - a field study to investigate effects on the earthworm fauna in maize in southern Germany.* Eurofins Report Number S08-00402.
Klein, O. (2010c) *Bicyclopyrone/S-metolachlor EC (A15936Y) - a field study to investigate effects on the earthworm fauna in maize in southern Germany*. Eurofins Report Number S08-01244.
Klein, O. (2013a) *Terbuthylazine/S-Metolachlor SE (A9476C) - a field study to investigate effects on the earthworm fauna in Spain.* Eurofins Report Number S12-00662.
Klein, O. (2013b) *Mesotrione/Terbuthylazine/S-Metolachlor SE (A13726E) - a field study to investigate effects on the earthworm fauna in Spain.* Eurofins Report Number S12-00663.
Kuntz, M., Berner, A., Gattinger, A., Scholberg, J.M., Mäder, P. & Pfiffner, L. (2013) Influence of reduced tillage on earthworm and microbial communities under organic arable farming. *Pedobiologia*, **56**, 251-260.
Lavelle, P. & Spain, A.V. (2001) *Soil Ecology*. Kluwer Scientific Publications, Amsterdam.
Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. & Rossi, J.-P. (2006) Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, **42**, 3-15.
Lewis, W.J., van Lenteren, J.C., Phatak, S.C. & Tumlinson, J.H. (1997) A total system approach to sustainable pest management. *Proceedings of the National Academy of Sciences*, **94**, 12243-12248.
Li, C.Y. & Nelson, E.E. (1985) Persistence of benomyl and captan and their effects on microbial activity in field soils. *Bulletin of Environmental Contamination and Toxicology*, **34**, 533-540.

Lofs-Holmin, A. (1982) Measuring cocoon production of the earthworm *Allolobophora caliginosa* (Sav.) as a method of testing sublethal toxicity of pesticides: An experiment with benomyl. *Swedish Journal of Agricultural Research*, **12**, 117-l 19.
Marinissen, J.C.Y. (1992) Population dynamics of earthworms in a silt loam soil under conventional and "integrated" arable farming during two years with different weather patterns. *Soil Biology and Biochemistry*, **24**, 1647-1654.
Martin, B.T., Jager, T., Preuss, T., Nisbet, R. & Grimm, V. (2013) Predicting population dynamics from the properties of individuals: A cross-level test of Dynamic Energy Budget theory. *American Naturalist*, **181**, 506-519.
McNaughton, S.J., Banyikwa, F.F. & McNaughton, M.M. (1998) Root biomass and productivity in a grazing ecosystem: the Serengeti. *Ecology*, **79**, 587-592.
MEA (2005) *Millenium ecosystem assessment, ecosystem and human well-being: synthesis*. Washington DC.
Montgomery, D.R. (2007) Soil erosion and agricultural sustainability. *Proceedings of the National Academy of Sciences*, **104**, 13268-13272
Owen, M.D.K. & Zelaya, I.A. (2005) Herbicide-resistant crops and weed resistance to herbicides. *Pest Management Science*, **61**, 301-311.
Pelosi, C., Bertrand, M., Makowski, D. & Roger-Estrade, J. (2008) WORMDYN: A model of *Lumbricus terrestris* population dynamics in agricultural fields. *Ecological Modelling*, **218**, 219-234.
Pittelkow, C.M., Liang, X., Linquist, B.A., van Groenigen, K.J., Lee, J., Lundy, M.E., van Gestel, N., Six, J., Venterea, R.T. & van Kessel, C. (2014) Productivity limits and potentials of the principles of conservation agriculture. *Nature*, **517**, 365-368.
Railsback, S.F. & Johnson, M.D. (2014) Effects of land use on bird populations and pest control services on coffee farms. *Proceedings of the National Academy of Sciences*, **111**, 6109-6114.
Scheu, S. (2003) Effects of earthworms on plant growth: patterns and perspectives. *Pedobiologia*, **47**, 846–856.
Spurgeon, D.J., Keith, A.M., Schmidt, O., Lammertsma, D.R. & Faber, J.H. (2013) Land-use and land-management change: relationships with earthworm and fungi communities and soil structural properties. *BMC Ecology*, **13**, 46.
Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. & Polasky, S. (2002) Agricultural sustainability and intensive production practices. *Nature*, **418**, 671-677.
van Capelle, C., Schrader, S. & Brunotte, J. 2012. Tillage-induced changes in the functional diversity of soil biota - a review with a focus on German data. *European Journal of Soil Biology*, **50**, 165-181.
van Groenigen, J. W., Lubbers, I. M., Vos, H. M. J., Brown, G. G., De Deyn, G. B. & van Groenigen, K. J. (2014) Earthworms increase plant production: a meta-analysis, *Scientific Reports*, **4**.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Netlogo programme code for the *Aporrectodea caliginosa* energy budget IBM.
Appendix S2. Default parameter values of the earthworm energy budget model.
Appendix S3. Details for modelling carbendazim effects on individual earthworms.
Appendix S3. Validation field trial details.
Appendix S4. Literature details used to model earthworm effects on crop yield.